Neural tube, Spheno-occipital Flexion and Semi-circular Canals in Modern and Fossil Hominids

Anne Dambricourt Malassé, Jean-Pascal Martin, Eric de Kerviler

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Neural Tube, Spheno-occipital Flexion and Semi-circular Canals in Modern and Fossil Hominids

Anne DAMBRICOURT MALASSE[1], Jean Pascal MARTIN [2], Eric de KERVILER [3]
(1. UMR 6569 CNRS, Laboratoire d'Anthropologie, Université Aix-Marseille II, Institut de Paleontologie Humaine, 1 rue Rene Panhard 75013 Paris, France; 2. Hopital Saint Louis, Service de Chirurgie Maxillo-Faciale, Paris, France ; 3. Hopital Saint Louis, Service de Radiologie, Paris, France)

Abstract

The position of the cartilaginous occipital, the sphenoidal angle, the frontalization of the petrous bone and the orientation of the foramen magnum, are major characteristics of basic-cranio-facial evolution in hominids. It has become standard to associate them and to notice their evolution or spatial organization according to the degree of spheno-occipital flexion. A study by scanning an ontogenetic series of *Pan* troglodytes and modern man's cranium, gives the first glimpse, with an application to complet fossilized craniums, or fragments of isolated petrous bone, such as Qafzeh (*Homo sapiens*), La Ferrassie and La-Chapelle-aux- Saints (*Homo neanderthalensis*), Sambugmacan and Solo 1 (*Homo erectus*). Paleontological and modern data indicate three groupings of around a same flexion: Great Apes, fossil *Homo* and Modern Man.

Key words: Computed tomography; Embryogeny; Hominids; Neural tube; Semi-circular canals; Sphenoidal flexion

The semi-circular canals are intra-cranial structures only accessible via radiography and better via Computed Tomography (CT scan). They each occupy a plane in space and form a right angle with the two other canals (figure 3). Recent studies conducted by Spoor, Zonneveld and Wind [1-2] showed angular divergences between adult Pan, *Australopithecus* and *Homo sapiens*. The lateral canal of *Homo sapiens* is further frontalized in relation to the posterior than in *Pan* and *Australopithecus*. This divergence has not been explained although it represents a major criteria of distinction between *Australopithecus* and *Homo*. This angular opening reaches the angular differences which have been noticed between cranial basis. Numerous works, such as those by Delattre and Fenart in the 1960s, have showed that the *Homo sapiens* cranium distingues itself from the *Paninae* (*Gorilla* and *Pan*) by a closer sphenoidal angle. They also showed the opening of this angle after the visible birth in all primates - at the exception of the modern man which remains in flexion, around a transversal axis of rotation.

They then noticed correlations between the value of the sphenoidal angle and the position of these three canals around the axis of rotation, and then between this same sphenoidal angle and the frontalization of the petrous bone. A closure of the adult sphenoidal angle, between the two present groups, seems to be correlated to a frontalization of the petrous bones and at a rotation of the two posterior and superior canal compared to the lateral canal taken as horizontal reference. What is the origin of this changes? And when do they occured in the phylogeny? Dean and Wood [3] found some of these correlations with *Australopithecus*. Indeed, the basis of the cranium shows a tri-dimensional architectural unit, distinct from the Great Apes, around a closer sphenoidal angle and a frontalization of the petrous more noticeable. We talk about the shortening of the cranial base, but the values are still superior to those of the *Homo* group. The correlations remain nonetheless visual and consensual, without any calculation of the correlation coefficient between the angles. In an other part, the interpretation of the differences is brought back to the hypothesis of the differential development of the cerebellar territory [4-5]. It is thus even more recently that Spoor, Zonneveld and Wind have applied the new technics of medical imaging to the study of thirteen fossil hominid cranium in two types, *Australopithecus* and *Homo*. The authors note the position of the otical capsul through the

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Biography : Anne DAMBRICOURT MALASSE (1959), paleo-anthropologist, Charge de Recherche of the National Center of Scientist Research (1990), Consulting in Archaeology, Foreign Office, Department of Social Sciences and Archaeology (1995-1996), Head of the Hindou Kouch Pak-French archeological prospection (1996-1998), Member of the National Council of University (1995-1999).

lateral canal, and evaluate the straightening of the clivus, the cranium placed in the Frankfurt plan. The orientation of the lateral canal remains the same for *Homo* and *Australopithecus*, it is close to 30°. Yet, the straightening of the clivus is largely more important in the *Australopithecus* than in the great Apes, but there does not appear to be different positioning between the lateral and posterior canals, at the difference of the *Homo sapiens*. *Homo sapiens* shows a straightening of the clivus even more marked and a new frontalization of the petrous.

To summarize, the slope of the clivus straightens with *Australopithecus*, according to an ascending antero-posterior rotation of the sphenoïdal corpus on one hand, and the petrous becomes frontalized, on the other hand. But the lateral and posterior canals remain linked together as in *Paninae*. The clivus further straightens with *Homo sapiens*, the petrous further frontalize again, and this time the lateral canal detaches itself from the posterior canal. Thus, there may exist a dynamic relationhip between the flexion amplitude of human and the detachment of the lateral canal. To understand the origin of these changes, the authors still remain in the hypothesis of an angular difference caused by a differential development of the neo-cortex of telencephalon or cerebellum "*The premize of all brain-size hypotheses is that because the cranial base is also the floor of the cranial cavity, brain size is a fundamental constraint on basicranial form*" [6-7]. This point of view is established on an late analysis of cranial ontogeny. At the first ontogenic stages, the cranial base is overlayed not by the telencephalic brain, but by the neural tube. We are going to attempt to understand the origin of the straightening of the clivus in *Homo sapiens*, and follow the formation of petrous, as well as the three semi-circular canals, by developping an ontogenetic approach, since the embryonic period [7]. We have discovered that the morphogenesis of the basic cranial form was well known still 1900, and that the most important angles are acquired during the seventh week. We have reach numerous works describing the neural and the chondrocranial developments, and presented a global synthesis. Then, we applied the study protocol of Monkeys, Great Apes and analyse fossilized hominids cranium.

Actually, numerous works have described the embryonic chondrocranium of human and monkeys since the beginning of this century, so that the compared anatomy of embryonic stages is possible. We could have thought that the straightening position of the clivus in a new born, is directely acquired during the ossification of the embryonic tissues. Yet, it is not the case. Like other mammals, in primate embryos (human included), the chondrocranium is flat. At the first embryonic stages, cartilageous tissues constitute the *planum basale* that is to say the spheno-occipital area, is plan. Levi [7] wrote as early as in 1900, the dynamic of this planum : during the seventh intra-uterine week, the sphenoidal part does a pivoting from top to bottom, back to forward, which thus brakes the rectitude of the planum and provoques a "plicature". At the beginning of the eighth week, the clivus, or the spheno-occipital slope, is acquired. The cartilageous tissues situated here and there of the sphenoidal body and the basi-occipital, that are the otic capsules, accompany the flexion. They will then translate by their positionning, the amplitude of this rotation. What is the origin of the sphenoidal rotation? The study of the neural tube growth trajectory underlying the chondrocranium, enables us to establish the dynamic correlations through the definition of an orthonorm analysis. This analysis is defined in lateral view. The chord defines the X axis, horizontal, and the apex defines the origin 0. The vertical axis Y, perpendicular goes through this apex (figure 1).

An elongation of the tube is observed forward of the chord, at the same time as the beginning of a prial rotation from the bottom to the top, from the front to the back, around an axis Z, perpendicular to the two other axes. The neural tissue pursues the spiral rotation and goes beyond the chordal area. It is at this precise stage, that the authors, among whom Levi, have described the spheno-occipital rotation. The chord follows the movement, the shenoidal angle then appears. And the otic capsules associated to the basi-occipital follows the movement. The differentiation of the canals begins at the end of the fourth embryonic week. At the sixth week, the three canals are distinct, but the lateral canal is still linked to the posterior; after the flexion, it is separated. We therefore conclude that strains generated by the elongation-rotation of the neural tube, determine the morphogenesis of the chondrocranium, first with the sphenoïdal flexion aimed on the apex of the

chord, then with lateral angular modifications such as those of the semi-circular canals. And it is therefore during the embryonic period, that one can trace the topographical differences between the different primate neuro-sphenoïdal dynamics. The phenomenon of rotation is common to all living primates, but the rotation of the chordal segment is less important in Monkeys and it is the entire basis of the cranium which is less bent. It will remain so during ontogeny. With the *Paninae*, *Gorilla* or *Pan*, comparison between an 8 month foetus of *Gorilla* and *Homo sapiens*, shows a sphenoidal angle more opened in the *Gorilla* than in the human, as well as a frontalization of the petrous and the posterior canal less marked. The origin of these angular divergences is therefore indeed linked to the intra-uterine morphogenesis of the cephalic pole. The embryonic brain of the *Gorilla* develops itself as in all primates, according to a spiral rotation of the neural tube which goes to the chord segment, but the rotation is of less amplitude than in human.

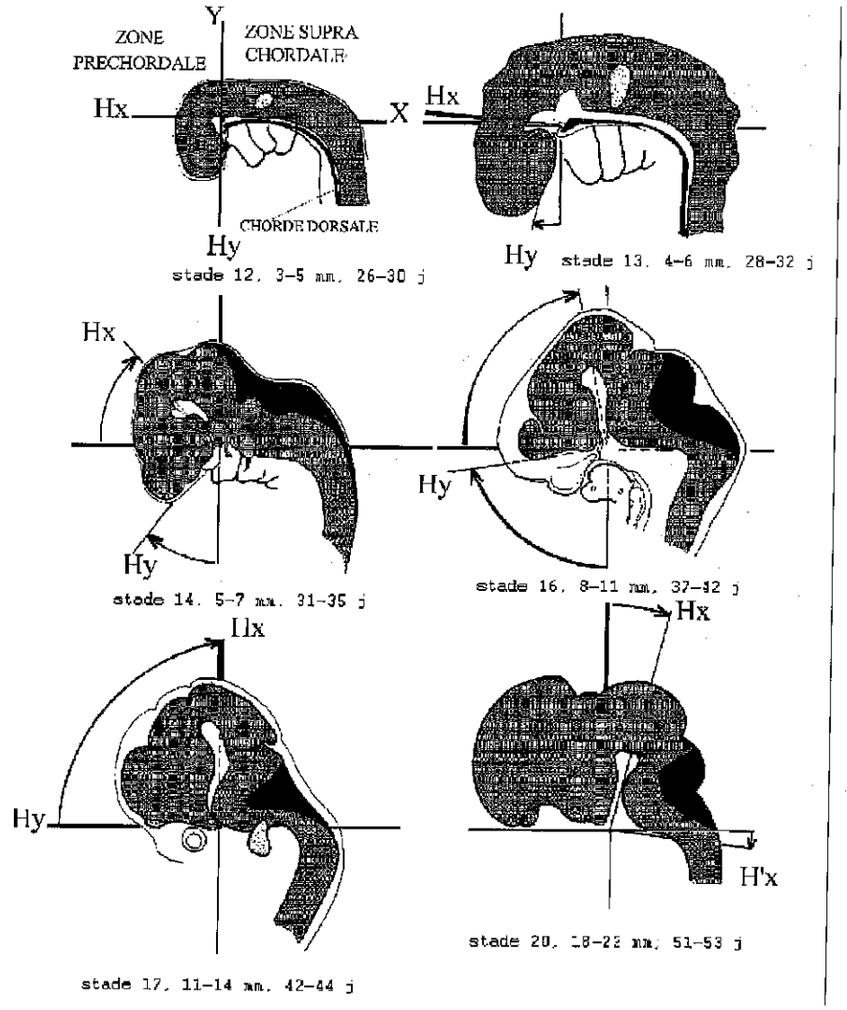

Figure 1 *Homo sapiens* neural rotation in lateral view [8]

It is obvious that fossil primates, including hominids, have developped from a flat chondrocranium and that they went through a rotation of the neural tube. It is the amplitude in the chord part which has changed, very week in the first Primate, it became more important stating with

the hominids. How do fossil craniums of *Homo* organize themselves according to this new key of understanding? In order to do so, the study material is made of cranium studied with X-rays and the CT scan for present species. Fossils are still in great majority studied from modern casts and exocranial measures. This study show the first result of the ontogeny of *Pan* and *Gorilla*, since the fetal stage.

In the first step, we test the correlation between the intra and exo-cranial angular values, in profile and transversal view, from present species, in order to establish predictions on the intra-cranial flexion in fossiles (figure 2). They will be verified by CTs studies, according to the degree of mineralization. The results [8] are close to May and Sheffer [9] who compare the sphenoïdal angle with an external angle, namely the cranio-facial flexion. The first sample is established for the radios of adult craniums of Gorillas, Chimpanzees and *Homo sapiens* taken radomly in a pluri-ethnical population. For the CTs, we study one adult *Homo sapiens*, a serie of six chimpanzees of growing age from the age of one year, a formol fetus and adult *Gorilla*. For the original fossils, the skulls are: *Homo sapiens*; Le Rond du Barry, Qafzeh 6, Qafzeh 7, *Homo erectus* from Indonesia Solo 1 and Sambungmacan (collection of Professor Teku Jacob) and *Homo* neanderthalensis, La Chapelle aux Saints. The second sample comes from casts only.

The results show first that for present species, two groups distinguish themselves according to the adult value of internal and external flexion, and the frontalization of petrous. Both groups are Sapiens and from its fossilized representatives, since Qafzeh, on one side, and the *Paninae* on the other hand, *Pan* et *Gorilla*.

Concerning the orientation of the petrous in external view, and the sphenoidal angle, at the adult stage, the coefficient of correlaton is the highest between *Gorilla* alone and *Homo sapiens* (0,8), it is of 0,7 between *Pan* and *Homo sapiens*. A closing of the sphenoidal angle between Great Apes and Human does indeed accompany a frontalization of the petrous.

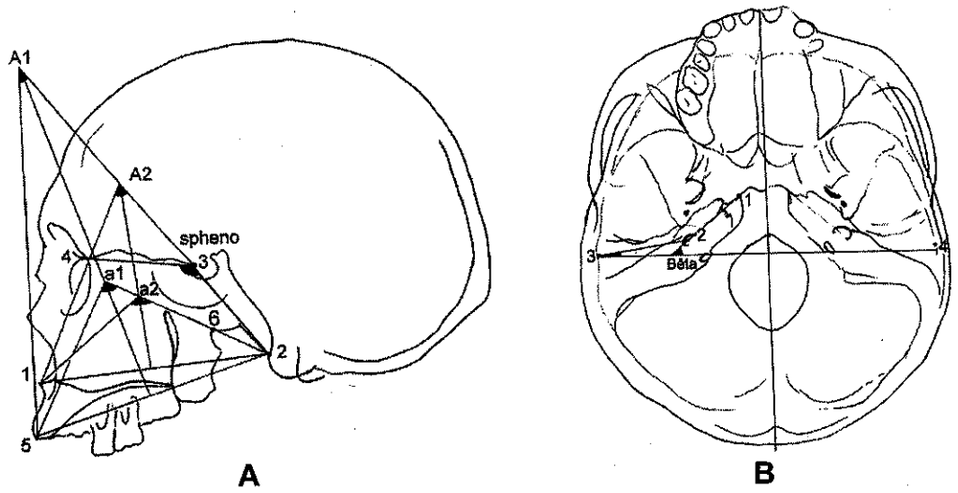

Figure 2 Khirgiz, IPH Collection, X Ray analysis

A: Basi-cranio-facial angular analysis: 1: external nasal spine, 2: basion, 3: tuberculum sella, 4: lame criblée, 5: prosthion, 6: hormion, A1, A2, internal craniofacial contraction, a1, a2, external cranio-facial contraction, spheno: sphenoïdal angle.

B: Petrous bone frontalization (beta) 1: intersection between the petrous bone and the clivus, 2: center of the carotidian canal, 3 and 4: porion

Table 1 angular measurements, external, internal cranio-facial contraction, sphenoïdal angle and petrous frontalization, in *Homo sapiens*, *Homo fossilis* and *Pan troglodytes*

Pan	A1	A2	béta1	Anglsphéno
A 194328	80	144	58	172
A1943 35	78	145	55	150
A 197415	79	153	55	161
1974 20	80	150	54	186
A 1919 9	80	142	53	151
A 194327	82	145	52	167
19 902	82	145	52	150
1974 16	85	152	51	148
1957 70	77	131	51	148
A 194326	76	138	50	162
Homo sapiens				
h-69-73-1	59	96	49	129
h-69-3-4	48	74	47	140
h-69-19-1	50	79	46	121
h-69-61-5	55	88	46	131
h-69-67-2	45	78	45	122
h-69-71-1	56	83	45	127
h-69-81-6	47	69	45	124
h-69-69-1	49	80	43	134
h-69-86-6	47	70	43	123
h-1872	53	85	41	132
A 1919 7	50	101	51	145
1969 3 1	42	84	33	135
1969 13 8	42	88	38	133
1969 61 7	50	107	39	136
A 1955 111	36	68	38	133
1955-101-1	59	95	37	135
1969 8 24	57	94	32	131
Homo fossilis				
ER3733	77	101	52	139
ER 3883	-	-	55	
Broken Hill	91	122	45	
OH9	-	-	45	
Nariokotome	88	98	49	
Petralona	78	110	47	
Dali	-	-	40	
Sangiran 17	100	122	43	
Ngandong	-	-	46	
Ngawi	-	-	55	
Sangiran Pit.4	-	-	50	
Saccopastore	90	114	35	
La Chapelle	108	132	35	
La Ferrassie	103	124		
SkhulV	88	115		
Cromagnon	94	113		

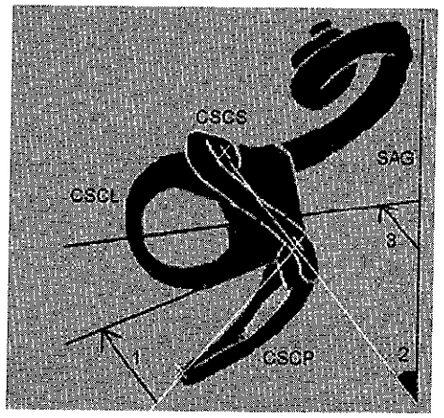

Figure 3 Angular measurements between semi-circular canals ; cscl: lateral semi circular canal, cscp: posterior semi circular canal, cscs: superior semi circular canal, ax: great axis of the lateral semi circular canal, sag: sagittal plane, X: cross section of the posterior and superior canals in the lateral canal plan

Concerning the semi-circular canals and the sphenoidal angle (figure 3):

- For the angular opening between the lateral and posterior semi-circular canals, the first measurements indicate a large difference of 20° between the child Chimpanzee of one year old and the adult *Homo sapiens*. Nonetheless, the value does not change during the post-natal ontogeny of the Pan, it varies from 9 to 11°, where the sphenoidal angle goes from 138° in a child less than 1 year old, and reach on average on 10 adults 160°. There appears a very clear rise of the semi-circular angle, three times superior in *Homo sapiens* than in Pan, with a sphenoidal angle closer which does not enter the variabilitiy of Pan. The double angular discontinuity is clear. May and Sheffer describe the same differences for the sphenoïdal angle, but they indicate an ontogenic stability in Pan, whereas it is classic to consider an increasing angulation. Nevertheless, a recent study [10] highlights a distinction during the deciduous period in *Paninae*, and observe a fast phasis of growth in the second part of this period. In orthodontics, a cranio-facial analysis applied to *Pan* and *Gorilla* describe the same phenomenon. At birth the *Paninae* are closed to the fetal growth, in terms of flexion, then during the deciduous phasis, the face begins to develop while the flexion stops.

- The frontalization of the lateral canal, given by its great axis relatively to the sagittal plane is the same in human and apes.

In fact, the differences between the semi-circular canals are not the lateral canal relatively to the sagittal plane but that of the posterior canal. Therefore, this angulation is acquired during the intra-uterine development. It is during their formation, at the pre-cartilageous stage, that the movement of canal translations in their own planes are possible. Since the orthogonality of the three canals are maintained, the possible margin of modification remains the position of the canals in their own planes, in the direction of verticality or horizontality. That is what we observe for the lateral canal between the Chimpanzee and the *Homo sapiens*. The closing of the sphenoidal angle is accompanied by this angular divergence. These results are in convergence with the thesis of a possible rotation of the lateral canal in its plane, at the moment of the spheno-occipital rotation, once it goes beyond the embryonic step which would be at the minimum the one of *Australopithecus*. In *Homo sapiens*, the greater flexion of the clivus could explain greater tension at the level of the posterior semi-circular canal which leads to a "sagittalisation", and not the frontalization of the lateral.

Dental stage of *Pan* : 1974-65 : dm2 unerupted 1974-33, c unerupted, 1974-35 M1 unerupted, 1974-51 M1 erupted, 1974-58 M2 erupted, 1974-29 M2 erupted.

Table 2

	Sphenoïdal angle	cscl/cscp angle (1)	Cscs/sagpl Angle (2)	Axcscl/sagpl angle (3)
Pan				
1974-65	142	11	38	55
1974 3	150	10	41	
1974-35	136	16	40	57
1974-51	158	15	37	50
Ado 1974 58		12	36	61
Ado 1974 29	151	12	31	51
Pan troglodytes				
Adulte	159,5			
n=10	[12,6]			
Gorilla fetus	164	12	45	46
Gorilla adulte	151			50
n = 12	[4,3]			
Sapiens	120	33		
n= 16	[12,6]			
Solo 1	-	33	47	58
Qafzeh 6		30		47
Sambungm				49

Concerning the casts of fossil hominids, the first exocranial measures of fossil *Homo* skull, indicates an external frontalization of the petrous more important than in *Australopithecus*, such as observed by Dean et Wood. It distinctly separates the craniums attributed to *Homo*, no matter the species considered. The frontalization is however even less than in Sapiens (table 2).

Concerning the originals fossils, the study of the semi-circular canals is precious because it compensates for the very frequent absence of the basi-cranium. The cranium of Qafzeh 6 shows a divergence of the lateral canal of 30°. The petrous of Qafzeh 7 is too mineralized to be analysed. The two craniums of *Homo erectus*, Sambungmacan and Solo 1, only Sambungmacan is usable, but the only accessible measure is the internal frontalization of the petrous of 46° which does not give any information on the flexion.

Neandertals are particular. A recent tomography of the juvenile petrous Arcy-sur-Cure [11], has permitted to notice a difference of position between the posterior canal, compared to the lateral, in the direction of verticality. The posterior canal went down, which is a characteristic found in La Chapelle-aux-Saints, La Ferrassie or La Quina. Yet, the application of a cephalometrical study in dynamic orthodontics [12], showed for La Chapelle-aux-Saints, a cranio-palatin equilibrium in extention relatively to the equilibrium of *Homo erectus* without any common point with Cro-Magnon or any contemporary *Homo sapiens*. Significant measurements of the basal skull are not the linear values, but the angular one. The Neanderthal basal skull is no longer than in modern *Homo sapiens*, thus this is not a shortening of the sphenoid which distinguishes Neanderthal from modern Man, as supported by Liberman, and discuted by Spoor *et al.* [13] but the sphenoïdal dynamics of rotation. This is found again with the larger *sella turcica*. The cranio-facial equilibrium is in extension relatively to *Homo erectus*. In this perspective, the low position of the posterior Neanderthalian canal could go in the direction of this basi-cranio-facial extension. The frontalization of the lateral canal is more important than in oldest skull, that is correlated with a greater external frontalization of the petrous. The entire sphenoïdal area in Neanderthals develops specific dynamics which has no equivalent in past, neither in modern human. A better understanding of the occipito-spheno-ethmoïdal dynamics, as developed by Deshayes [12] could explain the singularity of classic Neandertals. Our hypothesis is that such angular changes illustrate a modification of the embryonic neuro-sphenoidal dynamic of European *Homo antecessor* or *habilis* [7]. Then here, *Homo sapiens* is

no longer defined on empirical adult criterias such as the cranium capacity, but on more anterior datas which preceede telencephalization, not in the phylogeny, but in the ontogeny. The skull of modern man first appears as an embryonic evolution of the chondrocranium of *Homo* group, and not as a sub-species of the same embryonic organization. All the cranio-facial ontogeny is different. It would be interesting to study Dali [14], in the polycentric evolutionary perspective [15] while the fossil indicates a modern basal skull, but we notice a post-mortem compression effect. It would also be necessary to compare *Homo* antecessors with Qafzeh and the Neandertals.

To conclude, a systematic study of semi-circular canals would enable to introduce the embryonic dimension in the discourse on the evolutionary modalities, and to better define the belonging of a fossil to one phylum rather than another. In general, since the first hominids, from the Great Ape roots, it seems obvious that the chondrocranium presents itself as the reflection of an embryonic evolution relative to the neuro-chondrocranial dynamics.

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Enamel Microstructure of *Lufengpithecus lufengensis*

ZHAO Lingxia, LU Qingwu, XU Qinghua
(Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044 , PR China)

Abstract

The enamel microstructure of 5 permanent anterior teeth of *Lufengpithecus lufengensis* was observed with SEM. Incremental markings perikymata were clearly showed on the entire crown surface, and the density of perikymata showed a gradual increase towards the cervix. The crown formation times were estimated respectively using 7-days and 9-days periodicity of perikymata. Compared with fossil hominoids, modern humans and apes, crown formation time of *Lufengpithecus lufengensis* is close to that of *Australopithecus afarensis* and *Australopithecus africanus*, and closer to modern humans and apes; it is much longer than that of *Proconsul heseloni* and *Proconsul nyanzae, Australopithecus robustus* and *Australopithecus boisei*. The pattern of compactness of perikymata is similar to that of modern humans. Enamel prism patterns of *Lufengpithecus lufengensis* were observed. Concerning prism cross section patterns, Pattern 1 prisms occur in the very outer surface layer of enamel. Under super surface layer, Pattern 3 prisms predominate in the body of enamel, pattern 2 prisms are also found somewhere. In *Lufengpithecus lufengensis*, variants of pattern 3 exist, such as pattern 3A, 3B. It is strange and interesting that pattern 3B occurs at *Lufengpithecus lufengensis*, because up to date pattern 3B are recorded only in *Homo sapiens, Homo erectus* and *Australopithecus*, not found in extant and extinct apes. On longitudinal sections of enamel, Hunter-Schreger bands occur almost throughout the thickness from the enamel-dentine junction to the tooth surface. This is similar to *Homo*, and different from great apes. Of enamel microstructure, the preliminary results support the suggestion that *Lufengpithecus lufengensis* might be one of the members of hominoids related to early hominids.

Key words: *Lufengpithecus lufengensis*; Enamel microstructure; Incremental markings; Crown formation time; Prism patterns

1 Introduction

Studies of enamel structures and their implication to ontology and phylogeny have recently been realized by palaeoanthroplogists [1-2].

Two types of incremental growth lines are present within enamel: daily enamel prism cross-striation and circaseptan striae of Retzius or perikymata, these incremental markings provide an absolute timetable with which we can furthermore understand dental developmental events [3-5].

The ultrastructural unit of enamel is the prism, and prism patterns are an importance taxonomic tool. Scanning election microscopic analysis of enamel can provided new insights into hominoid evolution [6-10].

In this paper, enamel microstructure of *Lufengpithecus lufengensis* is addressed in (1) incremental markings and crown formation time, (2) enamel prism patterns.

2 Materials and Method

The materials are 4 isolated complete permanent teeth (one upper right incisor, one upper right lateral incisor, one lower right incisor and one lower left canine) and one permanent canine fragment. The observed position is placed on the lateral crown. For enamel prism pattern, according Gantt's [11] suggestion that the area of the tooth in which prisms are best arranged to study their pattern and organization is the mid-lateral crown area, a polished facet on the mid-lateral crown is etched with 0.1 M phosphoric acid for 40s. In addition, One bucco-lingual longitudinal section of the canine was prepared, in order to observe the cross-striations and shape and arrangement of enamel prisms. The specimen were analyzed with SEM (JSM-1600).

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Biography: ZHAO Linxia, currently carrying out the research on the microstructure of hominoids.